

A Preliminary Study on Phylogeny and Biogeography of the Family Paracortinidae (Myriapoda: Callipodida): a Cladistic Analysis

Daqing WANG

Department of Invertebrates, Institute of Zoology, Academia Sinica, Beijing 100080, P.R. China

ABSTRACT

The phylogeny and biogeography of a millipede family (Paracortinidae, fam. nov.) are preliminary examined by using a cladistic analysis. One of the 35 most parsimonious trees (cladograms), which also has the lowest (best) F value, is congruent with the scheme of evolution proposed by WANG & ZHANG (1993) from systematical analysis. Yunnan millipede *R. stimulus* is the sister group of all other extant Paracortinae. The other clade has the three Tibet species, *A. viriosum*, *A. serratum* and *A. carinatum* as the sister group of three Sichuan species, *P. voluta*, *P. leptoclada* and *R. thallinus*. The biogeography is inferred from the most parsimonious phylogenetic hypothesis of millipedes. The ancestral millipede in Yunnan moved first northward and diverged into two stocks. Subsequently, one of them moved eastward first and then vicariated into an eastern population and a western population. The another moved eastward and then separated into a western population and an eastern population. Some geological events are discussed for their possible effects in the formation of the present pattern of millipede distribution.

RÉSUMÉ

Phylogénie et biogéographie de la famille Paracortinidae (Diplopoda : Callipodida) : analyse cladistique préliminaire.

La phylogénie et la biogéographie d'une famille de diplopedes (Paracortinidae, fam. nov.) font l'objet d'une étude préliminaire à l'aide d'une analyse cladistique. L'un des 35 arbres les plus parcimonieux, qui présente la valeur de F la plus basse (la meilleure?), est congruent avec le bilan évolutif proposé par WANG & ZHANG (1993) à partir d'une étude systématique. Le diplopode du Yunnan *R. stimulus* est le groupe-frère de tous les autres Paracortinae. Trois espèces du Tibet, *A. viriosum*, *A. serratum* et *A. carinatum* constituent le groupe-frère de trois espèces du Sichuan, *P. voluta*, *P. leptoclada*, *P. thallinus*. Ils sont monophylétiques et constituent une trichotomie avec l'espèce du Yunnan, *R. stimulus*. La biogéographie est déduite de l'hypothèse de plus grande parcimonie pour les diplopedes. L'ancêtre des diplopedes du Yunnan s'est déplacé tout d'abord vers le nord et s'est divisé en deux stocks. Ultérieurement, l'un d'entre eux s'est d'abord déplacé vers l'est, puis a constitué une vicariance entre une population orientale et une population occidentale. L'autre s'est alors déplacé vers l'est et s'est séparé entre une population occidentale et une population orientale. La possibilité d'une influence d'événements géologiques dans la formation des modalités actuelles de la répartition des diplopedes est discutée.

INTRODUCTION

Cladistic analysis is a systematic method that attempts to discover genealogical (phylogenetic) relationships between taxa (HENNIG, 1966; WILEY, 1981). Since a detailed

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phylogenetic hypothesis for a group of organisms can and should serve as a basis for inferring the biogeographic history (HENNIG, 1966; BRUNDIN, 1966; NELSON & PLATNICK, 1981; HUMPHRIES & PARENTI, 1986), I have used this approach to study the phylogenetic relationships and biogeography of some millipedes (Callipodida: Paracortinidae). This paper preliminary reports some of these results, that will be precised in future works.

CHARACTER ANALYSIS

I chose the species of the genus *Eurygyrus* as the outgroup. From the analysis of morphology, the species of the genus *Eurygyrus* are close to the family Paracortinidae in affinities and the latter is rather ancient. This result can be derived from the descriptions of the morphological and diagnostic characters of the seven species of paracortinids. The morphological difference and diagnostic characters of the seven species were described in the paper, including the following ten characters listed in Table 1 (WANG & ZHANG, 1993). Table 1 gives the coding of morphological characters proposed for the paracortinid species, and Table 2 shows the matrix of the character states in the seven extant species of paracortinid millipedes. The branch and bound algorithm from the phylogenetic computer package PAUP 2.4.1, which guarantees the finding of all the most parsimonious trees, was used in this preliminary analysis.

TABLE 1. — Coding of the morphological characters for the seven paracortinid species.

Character	States of character: (code)
1. ratio of 4th-6th segments antennae	0: 1:1 1: < 1:1
2. process of 7th pair of legs in male	0: none 1: two
3. body color	0: dark brown 1: slight yellow
4. size of crests on collum	0: small and short 1: large and long
5. shape of collum edges	0: arch-shaped 1: parallel
6. shape of the median sclerite of hypoproct	0: rectangle 1: square
7. shape of eyes	0: ladder-shaped 1: triangular
8. gonopods	0: protrude from body 1: include in the body
9. concavity on front of head	0: deep 1: none
10. beak-shaped process in front head	0: none 1: large one

TABLE 2. — Matrix of character states in the seven new species of paracortinid millipedes. (Outgroup = genus *Eurygyrus*).

species	coding of characters									
	1	2	3	4	5	6	7	8	9	10
<i>R. stimulus</i>	0	0	1	0	0	0	0	0	0	0
<i>A. carinatum</i>	1	0	0	0	0	0	0	1	1	0
<i>A. viriosum</i>	0	0	0	1	1	0	0	1	1	0
<i>R. thallinus</i>	0	0	0	0	0	0	0	1	1	0
<i>P. voluta</i>	0	0	0	0	0	1	0	1	0	1
<i>A. serratum</i>	0	1	0	0	1	0	0	1	1	0
<i>P. leptoclada</i>	0	1	0	0	0	1	0	1	0	1
OUTGROUP	0	0	0	0	0	0	0	0	0	0

PHYLOGENY

A large number of trees (cladograms) was obtained, 35 in total, all with a consistency index of 0.636. The F value of these most parsimonious trees ranged from 0.155 to 0.611. However, there is only one tree with the lowest (best) F value, shown in Figure 1. BROOKS *et al.* (1986) suggested that the lower the F-ratio (= F value), the greater the degree of historical constraint on the data. In this regard, the tree with the lowest F value (Fig. 1) should exhibit the highest degree of congruence with the hypothesis of paracortinid evolution.

The phylogenetic hypothesis indicates that the Yunnan species, *R. stimulus* is the sister group of all other extant paracortinids. The species *A. carinatum* is the sister group of *A. viriosum* and *A. serratum*. The species *R. thallinus* is the sister group of *P. leptoclada* and *P. voluta*. Three Tibet species, *A. viriosum*, *A. serratum* and *A. carinatum*, and the three Sichuan species, *P. leptoclada*, *P. voluta* and *R. thallinus* are monophyletic and constitute the sister group that forms a trichotomy.

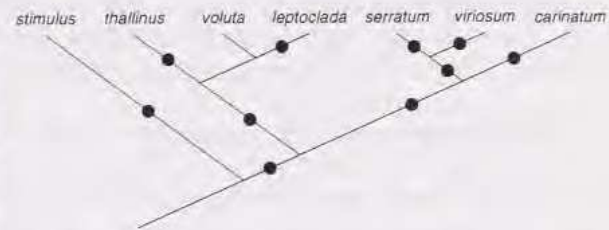


FIG. 1. — Cladogram showing hypothesized relationships among species of paracortinids.

Based on the fact that the setal patterns of Callipodida not only vary distinctly among different genera, but to a large extent correspond closely to groupings made on the basis of gonopod structure, (HOFFMAN, 1972), I propose the classification of the genera of the family Paracortinidae as follows:

g. *Paracortina*: *Paracortina leptoclada*, *Paracortina voluta*

g. *Relictus*: *Relictus stimulus*, *Relictus thallinus*

g. *Altum*: *Altum viriosum*, *Altum carinatum*, *Altum serratum*

Comparing this classification with the hypothesis, the only difference between them is the placement of the species *R. thallinus*, but the rest show the highest degree of congruence. This point would strongly support the cladogram shown in Figure 1. As for the difference, it is an interesting question and further study is needed.

BIOGEOGRAPHY

According to the principle of vicariance biogeography (NELSON & PLATNICK 1981; HUMPHRIES & PARENTI, 1986), a pattern of spatial distribution attained by the paracortinids can be deduced from the phylogenetic hypothesis. The area summary cladogram in Figure 2 illustrates how the present pattern of paracortinid distribution was attained.

According to the progression rule of HENNIG (1966), it implies that the ancestral paracortinid, residing in Yunnan, diverged into two lineages. One gave rise to the modern Zhongdian (Yunnan) species (*stimulus*, Fig. 2), and the other formed the species A (Fig. 2), which is the ancestor of all other extant paracortinid species. Species A migrated northward and then vicariated into two populations: the western population (B, Fig. 2) whose descendants later occupied Mongkang and Deqin (Tibet), and the eastern population (C, Fig. 2), whose descendants gave rise to all the paracortinids in Yiajang and

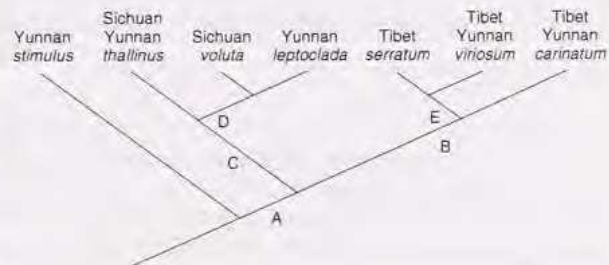


FIG. 2. — Area summary cladogram of paracortinids with ancestral species (A - E).

Batang (Sichuan). Species B migrated northward and then separated into the modern species *carinatum* and a species E, the ancestor of extant two Tibet species *serratum* and *viriosum*. Species C expanded eastward and diverged into the extant species *thallinus* and a species D, which is the ancestor of the extant two Sichuan species, *voluta* and *leptoclada*.

Geological events that cause fragmentation of a continuous ancestral distribution are considered the major reasons of distribution pattern formation (NELSON & PLATNICK, 1981). Although not all vicariant events are identifiable at present, the following are known geological events that could have produced the present pattern of paracortinid distribution.

Mong Kang and Deqin (Tibet) lie in a strip of land between two large rivers: the western Lancang River and the eastern Jinsha River. Batang and Yajiang (Sichuan) face the Jinsha River to the west and the Yalong River to the east. The three rivers flow rapidly so that it is not possible for paracortinids to cross. In other words, this vicariance took place before the emergence of the three large rivers.

The formation of the three rivers is the result of elevation of the Hengduan Mountains in the later Tertiary (PHYSIOGRAPHY OF CHINA, 1985). The fossil members of the order Callipodida indicate that callipodoids at least were widespread in Western Asia and North America (HOFFMAN, 1969). That is to say that it is very possible for paracortinids to migrate and diverge before the formation of the three rivers. The Tibetan species *leptoclada* and Sichuan species *carinatum* are being in Zhongdian (Yunnan) strongly support this idea.

The early paracortinid ancestor of Yunnan (Zhongdian) migrated northward before the Tertiary, then diverged into extant species *stimulus* and species A. Species A vicariated into western and eastern populations: Tibet species B and Sichuan species. Because of the emergence of the Lancang River and the Jinsha River, in the Tertiary, species B was separated, and then diverged into the extant species *thallinus* and a species D. The latter is the ancestor of species *voluta* and *leptoclada*. Species C was also separated in the later Tertiary because of the formation of the Jinsha River and the Yalong River. Then it diverged into the extant species *carinatum* and the species E, which is the ancestor of two species, *serratum* and *viriosum*.

CONCLUSION

The phylogenetic hypothesis of paracortinids (FIG. 1) presented in this work is the most parsimonious scheme derived from the cladistic analysis. It is congruent with the scheme of evolution proposed by WANG & ZHANG (1993). The vicariance model proposed for paracortinid biogeography is based on the adopted most parsimonious tree that shows congruence with the extant pattern of spatial distribution attained by paracortinids. The model interprets that (1) paracortinids arose in Zhongdian, Yunnan; (2) migrated northward before the Tertiary and then diverged westward and eastward; (3) because of the formation of three large rivers in the Tertiary, western and eastern populations were separated and then diverged into the extant paracortinids.

Nevertheless, it should be noted that the biogeographic hypothesis presented in this paper is to be considered as preliminary. More complete analysis will be proposed in future works.

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